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1 **Coupling of taxonomic diversity and morphological disparity in Devonian**  
2 **trilobites?**

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15 **Abstract**

16 Morphological disparity and taxonomic richness are two major aspects of evolution used to  
17 understand biodiversity changes. These metrics are often decoupled in time, particularly  
18 during the early history of clades. To assess the pervasiveness of this pattern during the post-  
19 acme of a clade, both morphological disparity and taxonomic diversity of the well-  
20 documented Devonian trilobites from North Africa were analysed. Morphospace occupancy  
21 and body size were estimated and compared to genus richness through time. This study  
22 highlights that, during the Early Devonian, morphological disparity of the pygidium and the  
23 cephalon strongly increased, whereas cranidium disparity remained low. Interestingly, the  
24 pygidium and cephalon morphological dynamics were decoupled. Taxonomic diversity also  
25 increased. Then, the Middle Devonian anoxic events affected the trilobite communities with  
26 simultaneous drastic loss of both morphologies and taxonomic richness. This coupling in  
27 diversity and disparity dynamics could be explained by either the intensity of extinctions or  
28 strong internal constraints. Finally, the weak Famennian recovery of both disparity and  
29 diversity did not reach the Early Devonian levels, thus making trilobites a ‘dead clade  
30 walking’ during their late evolutionary history. Devonian trilobite families **are thus identified**  
31 **as** ‘Top-Heavy Clades’, characterized by a diversity peak at the end of their history.

32

33 **Keywords:**

34 Trilobita;

35 Palaeozoic;

36 morphological disparity;

37 body size;

38 extinction;

39 palaeobiodiversity

40

## 41 **Introduction**

42 Studying successful clades (Alfaro et al. 2009; Benton 2015), such as the trilobites during the  
43 Palaeozoic, remains fundamental in macroevolution. Investigating and understanding such  
44 evolutionary success requires the consideration of taxonomic diversity, which estimates  
45 changes in the number of species through time, but also morphological disparity, which  
46 quantifies variation in morphology. The trilobites were probably among the most abundant  
47 marine macroinvertebrates during the Palaeozoic. Due to their high taxonomic diversity and  
48 their high morphological disparity, these arthropods constitute an important clade for  
49 documenting and testing macroevolutionary theories (Eldredge and Gould 1972; Foote 1991b,  
50 1993). They appeared and diversified during the Cambrian Explosion (ca. 521 Ma), exhibiting  
51 an important evolutionary success to become one of the major groups of the early Palaeozoic.  
52 However, the Hirnantian mass extinction (latest Ordovician), recognized as the first abiotic  
53 event, severely affecting them leading to a strong biodiversity decrease (Adrain et al. 1998).  
54 Whereas the trilobite taxonomic richness remained relatively stable in the Silurian, it changed  
55 importantly during the Devonian with, notably, a Pragian diversification followed by Middle  
56 and Late Devonian declines (Chlupáč 1994; Lerosey-Aubril and Feist 2012; Bault et al.,  
57 2022a). These biodiversity decreases took place in an unstable environmental context  
58 including quick sea-level fluctuations, anoxic/hypoxic events and climate upheavals (Walliser  
59 1996; House 2002; Joachimski et al. 2009; Qie et al. 2019). These environmental events  
60 mainly affected the marine faunas, including the trilobites (Feist 1991; Lerosey-Aubril and  
61 Feist 2012), and triggered major biotic crises such as the Kellwasser events and the  
62 Hangenberg event, and subsequently led to major ecosystem restructuring (Raup and  
63 Sepkoski 1982; Buggish 1991; Sepkoski 1996; Bond and Grasby 2017). Trilobites showed a  
64 low diversity in the late Palaeozoic, except for the last diversification in the Tournaisian, and

65 they completely disappeared at the end of the Permian (Lerosey-Aubril and Feist 2012). Thus,  
66 the Devonian constituted a key period in the evolutionary history of trilobites with important  
67 increases and decreases of diversity.

68 At the macroevolutionary scale, the taxonomic component of the palaeobiodiversity has  
69 been used traditionally as the major metric for a long time (Sepkoski 1978). However,  
70 numerous studies have shown the relevance of considering morphological disparity (Wills et  
71 al. 1994; Roy and Foote 1997; Foote 1997; Hopkins and Gerber 2017; Guillerme et al. 2020a)  
72 as an additional metric of biodiversity (e.g., Foote 1991a, 1993; Roy and Foote 1997; Neige  
73 2003; Adams et al. 2004, 2013; Hopkins 2013; Minelli 2016; Jablonski 2019). Morphological  
74 changes could even be a better proxy to understand extinction events (Wan et al. 2021).  
75 Indeed, while selective extinction lead to morphological disparity losses, non-selective  
76 extinction do not necessarily have the same effect (Foote 1991a; Puttick et al. 2020).  
77 Taxonomic richness and morphological disparity are often decoupled, the decrease in  
78 diversity can occur before the morphological disparity drop (Bapst et al. 2012) or, conversely,  
79 morphological disparity may decline before the taxonomic richness (Wan et al. 2021).  
80 Interestingly, studies on trilobite morphology were one of the driving forces behind the  
81 development of disparity analyses, notably with the pioneering work of Foote (Foote 1989,  
82 1990, 1991a). However, most of these works were based on the cranidium only. Further  
83 developments also focused on morphological modularity (Gerber and Hopkins 2011; Webster  
84 and Zelditch 2011; Oudot et al. 2019). Although trilobites quickly reached constant rates since  
85 the Cambrian after an initial period of high rate of morphological evolution (Paterson et al.  
86 2019), the peak of morphological disparity occurred in the Middle Ordovician, early in their  
87 evolutionary history (Foote 1991b, 1993). Then, the morphological disparity decreased, rather  
88 slowly until the Late Devonian and then sharply until their disappearance at the  
89 Permian/Triassic boundary. Despite a slight increase of their morphological disparity during

90 the Permian (Foote 1993), no important increase has been observed in trilobites as a whole.  
91 However, at a smaller taxonomic scale, trilobites could show reversible trends of intraspecific  
92 variation leading to new morphological diversification caused by different factors (Webster  
93 2007). Hopkins (2014) showed that environmental conditions such as climate and bathymetry  
94 can affect available morphologies, but these effects can also change through time. In addition,  
95 trilobite morphologies are known to be affected by developmental constraints such as  
96 heterochrony or enrolment (Hughes et al. 2006; Gerber and Hopkins 2011; Crônier 2013;  
97 Oudot et al. 2019).

98 In the Devonian, trilobites were abundant, diverse and well preserved. This is especially  
99 the case in North Africa where the conditions were favourable for their proliferation and  
100 scientist have been studying them for decades (Bault et al. 2021). Due to their richness, they  
101 constitute an invaluable fossil record (Alberti 1969, 1981; Lebrun 2018). During the  
102 Devonian, North Africa was located in the northern margin of the Gondwana supercontinent,  
103 and most of the area was covered by epicontinental seas related to the Palaeotethys Ocean  
104 (Guiraud et al. 2005). A major Early Devonian diversification was observed in this area  
105 before a decline in the middle Givetian (Bault et al. 2021) related to sea-level changes and  
106 anoxia (Kaufmann 1998). During the same period, numerous morphological innovations and  
107 morphological changes were also observed in trilobites from North Africa (Bault et al.  
108 2022b). Comparing the diversity and disparity leads to the exploration of large-scale  
109 biodiversity fluctuations, both in terms of patterns and processes, through time (Roy and  
110 Foote 1997) and space (Neige 2003). Therefore, the present study provides the first  
111 comparison between the taxonomic diversity and the morphological disparity of trilobites  
112 during the Devonian and known environmental fluctuations and global events (Joachimski et  
113 al. 2009; Becker et al. 2016). The relationship between these two metrics was investigated

114 more accurately by using an updated dataset at the regional scale, in the well-documented  
115 North African fossil record, and using the **geological** stage as the temporal resolution scale.

116

## 117 **Material and methods**

118

### 119 *Data*

120 Based on North African specimens (**Fig. 1A**) of trilobites illustrated in the literature, we  
121 compared the morphological dataset used in [Bault et al. \(2022b\)](#) and the associated taxonomic  
122 dataset. Analyses were performed on three key structures **concentrating most of the**  
123 **morphological variations**, i.e., the cephalon, the cranidium and the pygidium ([Whittington et](#)  
124 **al. 1997**). **The cranidium being often more preserved than the whole cephalon, we focused on**  
125 **this part to improve our dataset**. This study focused only on the central part of cranidium, **that**  
126 **is the glabella and the occipital ring** without the fixed cheek, named ‘central cephalon’ in  
127 [Bault et al. \(2022b\)](#). From the literature, we selected the specimens with complete structure  
128 with a sufficient resolution to be analysed. We only used dorsal views and the right side (or  
129 the left side by using mirror image if the preservation was better) for each structure.  
130 Consequently, we analysed respectively 308 cephalata, 943 cranidia and 604 pygidia for both  
131 diversity (i.e., taxonomic diversity) and disparity (i.e., morphological disparity) analyses.  
132 Only one cephalon and 35 cranidia used in our study correspond to early juveniles, i.e.,  
133 meraspid stages, the rest of the dataset corresponds to late juveniles or adults, i.e., holaspid  
134 stages. In order to account for the intraspecific variability, we studied all the specimens  
135 available with sufficient quality and not one specimen per species. The studied specimens  
136 represent 143 genera, 424 species and cover a period from the Ludlow to the Famennian (see  
137 supplementary material from [Bault et al. 2022b](#)).

138

139 *Figure 1 near here*

140

141 ***Geometric morphometrics, morphospace, and disparity***

142 The morphology of the three studied structures were investigated using geometric  
143 morphometrics with the acquisition of landmarks and semi-landmark coordinates (for a  
144 general overview of geometric morphometrics, see [Adams et al. 2004](#) and [Zelditch et al.](#)  
145 [2012](#)). Twenty two landmarks and one semi-landmark curve (i.e. glabella outline) were used  
146 to digitize each shape from published 2D illustrations (for the full list of used references, see  
147 [Bault et al. 2022b](#)). Fifteen landmarks were digitized on the cephalon, 7 on the cranidium and  
148 7 on the pygidium ([Fig. 1B](#); for the description and definition of these landmarks, [see Fig. S1](#);  
149 these landmarks correspond to key anatomical parts describing trilobite shapes and well-  
150 known to change through time and between clades). Six landmarks and the semi-landmark  
151 curve are common between the cephalon and the cranidium ([Fig. 1B](#)). The curve was  
152 automatically converted into a series of 16 equally-spaced semilandmarks. The digitization  
153 was performed using the software TPSdig ([Rohlf 2005, 2015; version 2.32](#)).

154 To remove the effect of size, location and orientation, the landmarked configurations [were](#)  
155 classically superimposed/standardized by using a generalized Procrustes analysis ([Gower](#)  
156 [1975; Rohlf and Slice 1990; Bookstein 1991; O'Higgins 2000; Zelditch et al. 2012](#)). The  
157 superimposed landmarks [were](#) projected to a linear tangent space at the full Procrustes mean  
158 ([Rohlf 1999](#)). Sliding of semi-landmark curves was done by minimizing the Procrustes  
159 distance ([Gunz & Mitteroecker 2013](#)). A principal component analysis (PCA) was performed  
160 to create a global morphospace, which depicts the relative shape similarity among studied  
161 trilobites (see [Bault et al. 2022b, Fig. S2](#)). Each specimen [was](#) thus characterized by a reduced  
162 number of variables and plotted along principal component axes (PCs), representing  
163 decreasing percentages of the total shape variance.

164 In order to quantify the morphological disparity through time based on the morphospaces,  
165 we used three disparity indices (Foote 1991a; Ciampaglio et al. 2001; Wills 2001; Guillerme  
166 et al. 2020b). Indeed, disparity indices are essential to assess the different aspects of disparity  
167 changes (Puttick et al. 2020) and can be characterized in three categories: the size, the density  
168 and the position of the morphospace occupancy (Wills 2001; Guillerme et al. 2020b). Here,  
169 computed indices related to the size of the morphospace occupancy are the sum of range  
170 (SoR) and the sum of variance (SoV). The SoR is an index of magnitude, corresponding to the  
171 total range of morphospace occupancy; it is sensitive to the sampling effort (Foote 1991a) and  
172 could be influenced by rare outlier morphologies (Deline 2009). The SoV is an index based  
173 on the variance of the specimens' position in the morphospace (Foote 1991b, 1993),  
174 measuring the average morphological dissimilarity among specimens; it is rather independent  
175 of outlier morphologies but more sensitive to the amount of sampled data (Foote 1991a). The  
176 Nearest-Neighbour Distance (NND) measures the density of the morphospace, this index  
177 corresponding to the shortest Euclidean distance between two points of a distribution of  
178 points. These various disparity indices have been computed for each considered Devonian  
179 time bins (geological stages). In addition to these raw values, which can be biased by the  
180 irregular sample size of published trilobites among geological stages, we also computed for  
181 each index its rarefied disparity by repetitive random subsampling without replacement (1000  
182 times) each time bin with the same number of specimens (confidence intervals are drawn at  
183 the 25 and 75 percentiles).

184 Environmental events are known to have an effect on the size of organisms, such as the  
185 size reduction known as the 'Lilliput Effect' (Harries and Knorr 2009). In a context of global  
186 environmental changes, we analysed whether size changes occurred in the Devonian. Here,  
187 specimen size was estimated as the natural logarithm of the centroid size (CS), which is the

188 square root of the sum of squared distances of all the landmarks from the centroid. Evolution  
189 of trilobite (centroid) size through time is investigated with traditional box plots.

190 These analyses were computed using R (v. 3.6.2; R Core Team 2019; [https://cran.r-](https://cran.r-project.org/)  
191 [project.org/](https://cran.r-project.org/)) and the ‘geomorph’ (v. 3.2.1; [Adams and Otárola-Castillo 2013](#)) and ‘epaleo’ (v.  
192 0.8.41; [Monnet, unpub.](#)) packages, as well as the ‘PAST’ software (version 3.24; [Hammer et](#)  
193 [al. 2001](#)).

194

### 195 *Taxonomic richness and comparison*

196 The taxonomic richness of studied trilobites was estimated with the sample-in-bin diversity  
197 (SIB; for a detailed discussion on palaeobiodiversity metrics, see [Foote, 2000](#); [Alroy, 2010a](#)),  
198 which corresponds to the raw count of taxa actually documented. Diversity was measured  
199 here as genus richness at the stage level. [Bault et al. \(2021\)](#) worked at the genus and species  
200 levels. They showed similar diversity trends, implying no effects of the taxonomic rank used  
201 for our analyses. The shareholder quorum sampling (SQS, [Alroy 2010b](#)) was also used to  
202 estimate the sampling-corrected diversity.

203 The strength of correlation between diversity and disparity indices through time was tested  
204 by means of the Kendall’s tau ([Kendall, 1938](#)) and *p* values were adjusted in case of multiple  
205 correlation to avoid false positives. Correlations were made from the Ludlow to the  
206 Famennian except for the Frasnian, which is characterized by a lack of data, for raw diversity  
207 and disparity, and for each phenotypic structure (cephalon, cranidium, and pygidium)  
208 separately. [Correlations were performed on both raw and detrended data to prevent false](#)  
209 [positives due to autocorrelations \(\[Ruta et al. 2013\]\(#\)\)](#). We used generalized difference of time  
210 [series to remove trends in time series data and eliminate autocorrelation by applying the](#)  
211 [method of G. T. Lloyd \(see: <https://graemetlloyd.com/methgd.html>\)](#)

212 Finally, comparison between morphological disparity and taxonomic richness during the  
213 Early Devonian diversification has been done following the bivariate method of Jablonski  
214 (2017). SIB, SoR and SoV have been standardized and are compared each other. Jablonski  
215 (2017) suggested that a higher increase of morphology than diversity suggests a less  
216 constrained developmental processes or exceptional ecological opportunities. This type 1  
217 diversification is typical of ‘early burst radiations’. Conversely, when the taxonomic  
218 diversification outstrips the morphological one, this type 3 diversification is rather a case of  
219 ‘non-adaptive radiation’. An intermediate diversification exists with concordant morphology  
220 and diversity increase, this is the type 2 diversification.

221

## 222 **Results**

223

### 224 *Taxonomic diversity*

225 The taxonomic richness showed the same trend between the three studied structures (Fig. 2;  
226  $\tau > 0.93$ ;  $p < 0.05$ ). Inherited from the reduced diversity of the Silurian, the diversity in the  
227 Lochkovian remained low, although it increased slightly, especially for pygidia. A sharp  
228 diversification occurred in the Pragian with an important increase of taxa followed by a  
229 deceleration in diversity that is variably marked according to the studied structures (less  
230 marked in pygidia, more marked in cephalia). Then the Emsian recorded the maximum  
231 diversity of mid-Palaeozoic trilobites, as illustrated by the impressive increase of the SIB  
232 index recorded through this stage (Fig. 2). Whatever the studied structure, the diversity began  
233 to decrease in the Eifelian before an even severe decline in the Givetian. Finally, the trilobites  
234 did not recover to their previous level of diversity despite a slight diversification in the  
235 Famennian. The diversity estimated with the SQS shows the same trends (Fig. S3).

236

237

*Figure 2 near here*

238

### 239 *Size of the morphospace occupancy*

240 The morphological disparity indices fluctuated differently according to the three studied  
241 structures (Fig. 3). Both raw data and rarefied values show the same trends. The rarefied SoR  
242 curves suggest little change in this metric over the period relative to the raw data. There was a  
243 low level of morphological extent in the Silurian characterized by very low values of SoR,  
244 SoV. An impressive increase of SoR index is recorded during the Lochkovian and Pragian  
245 (more impressive for cephalata than cranidia or pygidia), which reflects the filling of the  
246 morphospace. In the same time, SoV increased for the cephalon and the pygidium but not for  
247 the cranidium. While the SoR remained high during the Emsian for the three studied  
248 structures (Fig. 3a), only cephalata were characterized by high values of SoV (Fig. 3b). A  
249 morphological disparity peak occurred either in the Pragian or the Emsian depending on the  
250 metrics and the structure studied. Then, there was a slight decrease of morphospace  
251 occupancy in the Eifelian except for pygidia. The cephalata followed the pygidium trends  
252 considering the rarefied data. A substantial decrease of SoR index is subsequently recorded  
253 during the Eifelian–Givetian (more impressive for cephalata than cranidia or pygidia). A low  
254 level of morphological disparity characterized the Givetian (all indices, SoR and SoV, show  
255 very low values; Fig. 3a, b): morphospace occupancy collapsed in the Givetian for all  
256 structures. Then, a moderate increase of the SoV is observed during the Frasnian for the three  
257 studied structures (Fig. 3b). A moderate decrease of the SoR index is recorded in cephalata and  
258 cranidia, while an increase is recorded in pygidia (Fig. 3a). Nevertheless, in the absence of a  
259 sufficient number of specimens, this trend remains highly uncertain and should be treated  
260 with caution. In the Famennian, while the SoR continued to decrease for cephalata compare to

261 the Givetian (Fig. 3a), cranidia and pygidia show moderate increasing morphological disparity  
262 indices. SoV shows roughly similar trends (Fig. 3b).

263

264 *Figure 3 near here*

265

### 266 *Density of the morphospace occupancy*

267 The NND used as indicator of the density of the morphological occupancy is strongly  
268 influenced by the sampling effort as underlined by the very different raw and rarefied  
269 disparity curves (Fig. 3c). This is the only index showing major discrepancy in between raw  
270 data and rarefaction data. Indeed, the number of specimens strongly influences the density of  
271 the morphospace. The raw values result from the heterogeneity in numbers of species and  
272 individuals per genus, whereas rarefied data result from the same number of considered  
273 specimens among stages. The raw NND index sharply decreased in the Lochkovian for both  
274 cephalon and pygidia, while it increased for cranidia. As was the case for morphological  
275 occupancy indices, this density index shows an opposite trend for cranidia, for which it  
276 increased. Rarefied NND also increased for the cephalon, the cranidium and the pygidium. In  
277 the Pragian, the NND index shows very low raw values for the three studied structures  
278 suggesting an evolution from depopulated Lochkovian assemblages to reach Pragian ones.  
279 Conversely the rarefaction data show exactly the opposite. Rarefaction and raw values  
280 persisted at a plateau during the Emsian and rEifelian, two periods where many specimens  
281 were encountered in North Africa. The raw NND index subsequently increased during the  
282 Givetian and the Frasnian, followed by a decrease in the Famennian, although rarefaction  
283 values indicate the opposite. As with the other indices, the lack of specimens in the Frasnian  
284 prevents us from drawing robust conclusions. We used raw values trends in the discussion  
285 part.

286

287 *Size range*

288 There was no significant size changes in any of the structures through the studied period

289 (Kruskal-Wallis ANOVA:  $p < 0.05$ ), particularly regarding the cranidium (Fig. 4).

290 Nonetheless, some changes in the median centroid size and the interquartile distribution are  
291 observable. In the Silurian, the trilobites exhibited large cephalae and cranidia but small

292 pygidia on average as shown by their median centroid size (Fig. 4; see the thick lines);

293 similarly, the range of documented sizes is larger for cephalae and cranidia (Fig. 4a, b).

294 Subsequently, for cephalae and cranidia, the median size decreased strongly in the Lochkovian,

295 while, inversely, for pygidia it increased slightly (Fig. 4b): there was a loss of trilobites with

296 larger cephalae. In the Pragian, an increase in the median size began for cephalae and for

297 cranidia, and continued for pygidia: trilobites exhibited large morphologies than those found

298 in the Silurian. No changes in size are noticed in the Emsian, and only a slight size reduction

299 is recorded in the Eifelian. Major size changes are recorded in the Givetian with a more

300 important size range towards large trilobites with large cranidia and pygidia although the

301 median size remains similar to the size recorded in the Emsian (Fig. 4b, c). In the Frasnian,

302 only pygidia show a median size reduction. Nevertheless, compared to the Givetian, cephalae

303 and cranidia show an impressive reduction in the size range with the disappearance of the

304 largest morphologies. Subsequently, in the Famennian, cephalae and cranidia recorded an

305 impressive reduction of the median size (not observed in pygidia) and show an extensive

306 increase of their size range of the same order of magnitude as that observed in the Silurian or

307 the Lochkovian (Fig. 4a, b).

308

309

*Figure 4 near here*

310

311 ***Correlation between diversity and disparity***

312 The rank-based correlations between the various disparity and diversity indices are reported  
313 on **Table 1**. For cephalia, diversity trends are highly and significantly correlated to disparity  
314 trends for SoR, SoV and NND (not SoV and NND according detrended data). For cranidia,  
315 disparity and disparity trends are insufficiently correlated using SoV and NND, except for  
316 SoR. For pygidia, disparity and disparity trends are almost uncorrelated, using SoR, SoV and  
317 NND, but the SoV is correlated to raw diversity trends ( $\tau = 0.68$ ;  $p < 0.05$ ). Size of the  
318 trilobites was poorly and not significantly correlated to diversity whatever the structure  
319 studied ( $\tau < 0.5$ ;  $p > 0.05$ ).

320

321 *Table 1 near here*

322

323 ***Diversification modes***

324 The morphological disparity for the cephalon, the cranidium and the pygidium increased  
325 rather simultaneously during the Early Devonian diversification (**Fig. 5**). This places the  
326 Devonian trilobites of North Africa in the type 2 diversification of Jablonski (2017).  
327 Nonetheless, the SoV of the cephalon and the cranidium showed higher variation than the  
328 taxonomic richness, suggesting a potential type 1 diversification (**Fig. 5a,b**). Conversely, the  
329 SoV of the pygidium increased less than the diversity index, indicating a link with the type 3  
330 diversification (**Fig. 5c**).

331

332 *Figure 5 near here*

333

334 **Discussion**

335

336 *Diversification: diversity vs. disparity*

337

338 Both morphological disparity and taxonomic richness were very low at the end of the Silurian.

339 The low sampling characterizing the late Silurian makes the morphological trends uncertain in

340 the beginning of the studied period. However, the rest of our biodiversification trends are

341 quite robust with a good sampling through the Devonian. Thus, trilobites underwent two

342 periods of diversification in the Devonian, at the regional scale of North Africa as at the

343 global scale (Chlupáč 1994; Lerosey-Aubril and Feist 2012; Bault et al. 2021): in the Early

344 Devonian and in the Famennian (latest Devonian). However, these two periods of

345 diversification varied in intensity and duration.

346 During the Early Devonian, morphological disparity slightly increased in the Lochkovian,

347 but the most important rise in diversity and disparity occurred in the Pragian. This stage

348 corresponded to the onset of the Early Devonian diversification (Chlupáč 1994; Bault et al.

349 2022a), which arose from the basal Pragian regression that led to the development of shallow

350 carbonate environments (Chlupáč and Kukul 1986). The morphospace density also

351 progressively increased in the Lochkovian and the Pragian, particularly for the cephalo,

352 suggesting the proliferation of taxa with rather similar shapes. This corresponded especially to

353 the proliferation of some families such as proetids, tropidocoryphids, phacopids and

354 scutelluids (Bault et al. 2021). Macroevolutionary studies showed that a simultaneous increase

355 in diversity and morphological disparity can reflect an adaptive radiation (Foote 1993, 1997).

356 Furthermore, an increase in disparity is generally linked to an increase in ecological

357 differentiation (Cole and Hopkins 2021). However, Bapst et al. (2012) emphasized the

358 necessity to perform more detailed analyses to confirm this hypothesis. In the case of North

359 Africa trilobites, clades rapidly colonised new environments and diversified both in terms of

360 diversity and disparity with the expanding of epicontinental seas (Morzadec 2001; Bault et al.

361 2021). Such colonisation can correspond to the empty ecospace hypothesis (Erwin 1993;  
362 Ciampaglio 2002; Hughes et al. 2013; Novack-Gottshall 2016). Indeed, exceptional  
363 ecological opportunities could even lead to a higher rate of morphological evolution during a  
364 diversification (i.e., Type 1 diversification, Jablonski 2017). Moreover, phenotypic plasticity  
365 could boost diversity increase with new environmental opportunities, although its role on  
366 disparity remaining uncertain (Minelli 2016). However, Devonian trilobites were rather in a  
367 case of concordant morphological and taxonomical diversification (i.e., Type 2  
368 diversification, Jablonski 2017, Fig. 5), an intermediate diversification between ‘early burst  
369 diversification’ and ‘non-adaptive radiation’ (Jablonski 2017). The decoupling between the  
370 body size and the genus diversity also suggests that the Devonian diversification was not  
371 adaptive (Ramírez-Reyes et al. 2022). Nevertheless, it implied a radiation favoured by new  
372 environmental niches, such as shallow and siliciclastic environments (Chlupáč 1994;  
373 Morzadec 2001). Some novelties appeared such as spines (Bault et al. 2022b). Thus, although  
374 the trilobite size increased not significantly in the Pragian, cephalata and pygidia seemed to  
375 enlarge.

376 With the persistence of favourable environments, particularly in North Africa, the trilobites  
377 continued to diversify until they reached a diversity peak in the Emsian (Chlupáč 1994; Bault  
378 et al. 2021). During this period of intense taxonomic diversification, the morphological  
379 disparity still increased for both cephalon and cranidium. An increase of the morphospace size  
380 (SoR) shows that it corresponds to the appearance of new morphologies on the edges of the  
381 pre-existing morphospace (Ricklefs and Miles 1994; Roy and Foote 1997). It corresponds in  
382 particular to the development of morphologies with both sagittal and genal spines (Bault et al.  
383 2022b). Indeed, the diversification of scutelluids contributed to the extension of the  
384 morphospace occupancy with the development of long sagittal pygidia with a small rachis  
385 (Bault et al. 2021). This proliferation of morphologies with spines among Early Devonian

386 trilobites was interpreted as a potential response to increasing nekctic predation (Brett 2003) in  
387 the frame of the Devonian Nekton Revolution (Klug et al. 2010). However, a decrease of  
388 ecological opportunities can slow-down the rate of morphological evolution (Mahler et al.  
389 2010; Hopkins 2013). Trilobites having invaded most of the ecological niches appearing in  
390 the Pragian (Chlupáč 1994), it may explain the lower increase in disparity in the Emsian (or  
391 even the decrease depending on the structure and the metric observed). Indeed, the pygidium  
392 reached its maximum disparity in the Pragian, while the cephalon continued to differentiate  
393 until the Emsian. Trilobites still diversified morphologically but particularly on the cephalon.  
394 Hence, the morphological disparity of the pygidium and the cephalon became decoupled. This  
395 explains why both cephalon and cranidium were closer to the Type 1 diversification of  
396 Jablonski (2017), whereas for the pygidium the morphological diversification was lower than  
397 the taxonomic one. A larger cephalon diversification was possible because the cephalon was  
398 devoted to a wider range of morphofunctional tasks, including feeding habits (Fortey and  
399 Owens 1999) and visual ability (Clarkson 1975; Schoenemann 2021). Nevertheless, it can be  
400 claimed that the cephalon morphology was more constrained because it supported key  
401 functional structures and perform key tasks (Agrawal et al. 2010).

402 The second period of diversification that occurred in the Famennian (Lerosey-Aubril and  
403 Feist 2012; Bault et al. 2021) was less intense than the Early Devonian diversification. This  
404 stage follows the low-sampled Frasnian stage, making morphological disparity trends in the  
405 Late Devonian difficult to interpret. Nevertheless, the Famennian peak of taxonomic richness  
406 occurred after a period of low diversity due to the Kellwasser events, a series of rapid sea-  
407 level changes and anoxia causing mass extinction of marine organisms (Feist 1991; Chlupáč  
408 1994; Lerosey-Aubril and Feist 2012; Bault et al. 2021). Unlike the Early Devonian  
409 diversification, in which five orders contributed to the diversity peak, only two orders (i.e.,  
410 Phacopida and Proetida) participated in the Famennian diversity peak. No new morphologies

411 developed during the Famennian recovery, except a slight increase of cranium and  
412 pygidium disparities. The decrease in the morphospace density suggests a clustering trend  
413 among the Famennian trilobites (Foote 1990; Wills 2001). The absence of a disparity burst  
414 after the Kellwasser mass extinction indicate that biological constraints such as competing  
415 clades did not disappear (Oyston et al. 2015). A recovery with few innovations was also  
416 reported in other clades like graptolites (Bapst et al. 2012).

417

#### 418 *Extinction: diversity vs. disparity*

419

420 The diversity strongly dropped during the Middle Devonian of North Africa. At the global  
421 scale, the Middle Devonian ecosystem faced several extinction events such as the Eifelian  
422 Choteč and the Kačák events and the Givetian Taghanic event (Walliser 1996; House 2002).  
423 Sea-level rise and anoxic/hypoxic conditions characterized these events (Kaufmann 1998;  
424 House 2002). At the North African scale, these successive events led to the loss of many  
425 genera and families within trilobites (Bault et al. 2021). This decrease began in the Eifelian to  
426 reach a minimum of diversity in the Givetian. The morphological disparity was not affected  
427 immediately and most of the morphospace occupancy persisted in the Eifelian. Nevertheless,  
428 the increased extinction in the Givetian also strongly disturbed morphological disparity.  
429 Therefore, although the Choteč event greatly affected other invertebrate faunas in the  
430 Moroccan area (Becker and Aboussalam 2013), the following Kačák and Taghanic events had  
431 a stronger effect on trilobite morphologies. In particular, the Taghanic event corresponded to a  
432 global faunal overturn due to rapid eustatic changes and overheating pulses, which affected  
433 Moroccan trilobites (Aboussalam and Becker 2011). Noteworthy, this delay in the  
434 morphological disparity loss compared to taxonomic diversity was not specific to trilobites.  
435 Within the macrobenthos, diplobathrid crinoids showed the same pattern with only a slight

436 morphological **disparity** loss in the Eifelian despite an important diversity decrease and, then,  
437 followed by the major morphospace collapse occurring later (Cole and Hopkins 2021).  
438 Henceforth, the Middle Devonian events led to several shape losses among trilobites resulting  
439 in a strong reduction of both morphological range and variance. These changes indicate a non-  
440 random extinction (Ciampaglio et al. 2001). **This pattern contrasts** to the early Palaeozoic  
441 decline during which extinctions were not morphologically selective, leading to the  
442 decoupling of disparity and diversity (Foote 1991a, 1993; Hopkins 2013). The shape losses  
443 among trilobites correspond especially to the disappearance of trilobites with genal spines  
444 such as the aulacopleurid *Cyphaspides* or the asteropygin *Mrakibina* (Bault et al. 2022b;  
445 Morzadec 2001; Chatterton et al. 2019).

446 During the Late Devonian diversity and disparity patterns are more difficult to analyse  
447 because of a lack of data in the Frasnian. North African trilobites seem to decrease their  
448 morphological disparity during the Late Devonian Kellwasser extinction events, which were  
449 one of the five major extinction events in the life history on Earth (Raup and Sepkoski 1982;  
450 Buggisch 1991; McGhee 1996; Racki 2020). The cephalic morphologies were the most  
451 affected in North Africa, notably with the disappearance of the remaining spiny shapes such  
452 as the genera *Gondwanaspis* or the trilobites with large cephalic shields such as harpetids  
453 (Feist 2002). The density of morphologies seemed not strongly affected by this decrease,  
454 suggesting only marginal or lateral extinctions (Foote 1991a; Korn et al. 2013). Consequently,  
455 not all the trilobite taxa were affected in the same way. In North Africa and also at the global  
456 scale, the most impacted taxa were member of the orders Lichida, Odontopleurida, Harpetida  
457 and Corynexochida, which disappeared before the Famennian (Feist 1991; Lerosey-Aubril  
458 and Feist 2012; Bault et al. 2021).

459 In addition to extinction, ecological constraints can also limit morphological disparity  
460 (Oyston et al. 2015). Thus, a long-term eustatic rise associated to rapid transgressions

461 affected the Middle and Late Devonian faunas (Johnson et al. 1985; Kaufman 1998; House  
462 2002) and led to a decrease of the trilobite speciation rate by increasing geographic range  
463 (Abe and Lieberman 2009). The morphological disparity was also partly linked to  
464 environmental heterogeneities or changes (Hopkins 2014; Bault et al. 2022b), a harmonization  
465 of environment may led to a decrease in the morphological disparity. This trend was not  
466 compensated by local variations in the environment (Bault et al. 2022c). On the over hand,  
467 ecological stresses induced by unfavourable environmental changes could lead to increasing  
468 intraspecific variability (Crônier et al. 2015). Such ecological stresses could also be caused by  
469 the development of potential predators in the second half of the Devonian leading to selective  
470 extinction (Brett 2003; Johnson and Belk 2020). We can notice the indirect disappearance of  
471 the spines that have become ineffective (Brett, 2003; Bault et al. 2022b). Non-random  
472 extinction in North African trilobites is consistent with standard environmental changes,  
473 whereas catastrophic events such as the end-Permian extinction were non-selective (Villier  
474 and Korn 2004). In addition, a potential saturated taxonomic richness could favour such a  
475 decline, while the diversity reached its maximum during the Emsian (Bault et al. 2021). Self-  
476 regulation during a period of high diversity has been previously reported among trilobites  
477 (López-Villalta 2016).

478

### 479 *Size*

480 Changes in body size of organisms through time, either with a sudden decrease following an  
481 extinction event (known as the ‘Lilliput effect’ (Girard and Renaud 1996; Twitchett 2007;  
482 Harries and Knorr 2009), or with a long-term increase (known as the ‘Cope’s rule’; Stanley  
483 1973; Alroy 1998; Heim et al. 2015) have been documented repeatedly in the fossil record  
484 (Bell 2014). On the one hand, a Lilliput effect was recorded for different crises and different  
485 clades (Twitchett 2007; Song et al. 2011; Brom et al. 2015; Berv and Field 2018; Wiest et al.

486 2018 among other) among which are some arthropods (Forel et al. 2015; Chu et al. 2015;  
487 Martínez-Díaz et al. 2016). On the other hand, it has not yet been reported among trilobites,  
488 although a decrease in size already affected trilobites at a regional scale, for example in  
489 Norway during the Late Ordovician (Sigurdson and Hammer 2016). In the Devonian, such  
490 decrease in size was reported in other clades during the early Givetian (Bosetti et al. 2011;  
491 Comniskey et al. 2016; Zhuravlev and Sokiran 2020). Eifelian–Givetian and Famennian  
492 corresponded to two post-crisis periods for North African trilobites (Bault et al. 2021) but no  
493 important size decrease occurred. In contrast, Givetian trilobites were among the largest  
494 Devonian trilobites with the presence of the genera *Hypsipariops* and *Drotops* (Struve 1995).  
495 Their disappearance after the Taghanic transgression corresponded to the only period  
496 characterized by size reduction within Devonian trilobites (Crônier 2013). In a context of sea-  
497 level rise, presence of large trilobites could have resulted from the invasion of deep  
498 environments like North African Ordovician trilobites (Saleh et al. 2021). However, in this  
499 case, these phacopids represent assemblages adapted to unstable, high-energy environments  
500 of shallow internal platforms, explaining their disappearance after the Taghanic transgression.  
501 In the Eifelian and in the Famennian, the average size decreases, but only slightly and not  
502 significantly, and large trilobites remained present. Hence, it appears that no ‘Lilliput effect’  
503 affected North African trilobites in the Middle and Late Devonian events. However, our  
504 stage-based study might not be precise enough to identify such a pattern.

505

### 506 *Coupling in diversity and disparity patterns?*

507

508 At the global scale, the Early Devonian represents the second most important period of  
509 diversification of trilobites, after the initial Cambrian radiation (Adrain 2008). This bimodal  
510 evolutionary radiation was not unique, being found in other taxa (i.e., dinosaurs, crinoids) and

511 periods (i.e., Mesozoic and Cenozoic) (Romano et al. 2018; Romano 2021). The Devonian  
512 diversification was different to the early Palaeozoic diversification which was characterized  
513 by decoupled diversity and disparity (Foote 1993). On the one hand, the Cambrian–  
514 Ordovician was the early evolutionary history of trilobites, and the increase of their diversity  
515 corresponded to the appearance and the development of new orders (Fortey 2001; Paterson et  
516 al. 2019). On the other hand, the Devonian diversification occurred at low taxonomic ranks  
517 (family and below) within orders, which already existed since the early Palaeozoic (Chlupáč  
518 1994; Bault et al., 2022a). Devonian morphologies were less constrained during their  
519 ontogenetic development during the Cambrian than during the Devonian (McNamara 1986;  
520 Hughes 1991, 2007). In addition, trilobites exhibited greater morphological variation early in  
521 their evolutionary history (Webster 2007). These differences could explain why  
522 morphological innovations stopped increasing at the same time as diversity during the  
523 Devonian. Additionally, the trilobite moulting behaviour showed the same decreasing pattern  
524 with the disappearance of ventral sutures and the increasing importance of the cephalon  
525 moulting to the detriment of the other moulting characteristics (Drage 2019). Thus, the  
526 concordant increase in diversity and disparity observed during the Early Devonian differs  
527 from the ‘early burst’ diversification model, which is characterised by higher rates of disparity  
528 as observed during the Cambrian-Ordovician (i.e., Type 1 diversification of Jablonski (2017)).  
529 Because a higher level of constraint limits innovations (Oyston et al. 2015), the morphological  
530 disparity did not increase after the Emsian diversity peak. This pattern was already reported  
531 among trilobites during the Ordovician diversification when Phacopida showed simultaneous  
532 morphological and taxonomical changes (Foote 1993). This coupled diversity and disparity  
533 dynamics has been documented in other marine organisms during the Palaeozoic such as the  
534 diplobathrid crinoids (Cole and Hopkins 2021).

535 The early Palaeozoic and the Devonian also differ according to their post-acme diversity  
536 patterns. In the Early Palaeozoic, after its taxonomic richness peak, trilobite diversity  
537 decreased progressively before a stronger decline in the Hirnantian ([Adrain et al. 1998](#);  
538 [Sheehan 2001](#); [Fan et al. 2020](#)). Conversely, trilobite diversity decreased sharply in the  
539 Devonian ([Lerosey-Aubril and Feist 2012](#); [Bault et al. 2022a](#)). This dynamic was not specific  
540 to trilobites because the crinoid and conodont diversifications were also interrupted abruptly  
541 by the Devonian extinction events ([Ginot and Goudemand 2020](#); [Cole and Hopkins 2021](#)).  
542 Consequently, the potential protracted increase in disparity during the Devonian could be  
543 prevented by extinction events and, consequently, the coupling between changes in diversity  
544 and disparity could be an artifactual pattern.

545

#### 546 *Dynamics and macroevolutionary patterns*

547

548 [Gould et al. \(1977\)](#) defined an index to identify if the clades were more diverse before, after  
549 or midway through their evolutionary history. Although the early Palaeozoic clades, including  
550 trilobites, showed greater diversity in their early evolutionary history and are characterized as  
551 ‘bottom-heavy’ clades ([Gould et al. 1987](#)), North African trilobites showed an increase in  
552 both diversity and morphological disparity in the Devonian. This diversification was unusual  
553 because of diversification at low taxonomic ranks, especially within families and subfamilies  
554 such as phacopids, proetids or acastids, which appeared in the Ordovician more than 35 Myr  
555 before ([Adrain 2013](#)). Evolutionary rates are often higher in the early history of clades  
556 ([Hughes et al. 2013](#)) because of a progressive slowdown due to an important morphological  
557 space saturation ([Foote 1994](#); [Villier and Eble 2004](#)), decrease of ecological opportunities  
558 through time ([Erwin 1993](#); [Foote 1997](#)) and internal constraints ([Wagner 2000](#); [Oyston et al.](#)

559 2015). However, the evolutionary rates varied through time, and other patterns such as  
560 ecomorphological shifts occurred (Hopkins and Smith 2015).

561 Subsequently, a strong decline of diversity and morphological disparity occurred in the  
562 second part of the Devonian. Most of the trilobite families disappeared before the  
563 Carboniferous with the exception of proetids (Lerosey-Aubril and Feist 2012). Hence, most  
564 Silurian and later clades had higher taxonomic richness midway through their history, and are  
565 characterized as symmetrical clades, or later through their history and are characterized as  
566 top-heavy clades (Gould et al. 1987).

567 After the peak of both diversity and disparity in the Emsian, trilobites strongly declined  
568 and never reached their previous taxonomic and morphological richness. The Middle  
569 Devonian extinctions occurred at both regional and global scale at low taxonomic ranks  
570 among trilobites (Lerosey-Aubril and Feist 2012; Bault et al. 2021). However, the demise of  
571 several families and orders occurred later, in the Frasnian (Feist 1991). Some extinctions led  
572 to evolutionary bottlenecks with a reduction of the morphological and taxonomic  
573 diversification afterwards, like the Late Devonian extinction (Sallan and Coates 2010; Cole  
574 and Hopkins 2021). The disappearance of taxa can trigger new diversification events leading  
575 to increase ecological opportunities (Erwin 1993, 2001). With regard to the trilobites in  
576 particular, the Devonian extinctions hampered the subsequent great diversification (Lerosey-  
577 Aubril and Feist 2012) and the new opportunities were not sufficient to reverse this trend, as  
578 for Early Triassic anomodonts (Ruta et al. 2013). The time span between the numerous  
579 genus extinctions in the Middle Devonian and the demise of most of the families in the Late  
580 Devonian indicates that trilobite families are ‘dead clades walking’ (DCW Jablonski 2002).  
581 Only the order Proetida, which showed another important diversification later, in the  
582 Tournaisian (Lerosey-Aubril and Feist 2012; Bault et al. 2022a), did not exhibit a DCW  
583 pattern. Because Phacopida survived more than one stage after the Middle Devonian

584 extinction, they were not strictly a DCW (Jablonski 2002) but they showed a similar pattern.  
585 Nevertheless, Barnes et al. (2021) extended the concept to longer duration, impacts of mass  
586 extinction having longer influence than expected. This is partly due to the long-term impact of  
587 selective extinctions on the trait distributions of later species (Puttick et al. 2020). Although  
588 trilobites slightly recovered after the Kellwasser events (Feist 2019), they remained poorly  
589 diversified in the Famennian in North Africa (Fig. 2, Bault et al. 2021) as well as at the global  
590 scale (Chlupáč 1994; Bault et al. 2022a). On the contrary, many clades recovered strongly in  
591 the Famennian, among which many nektic organisms (Klug et al. 2010) and some benthic  
592 organisms such as echinoderms (Waters and Webster 2009). Other taxa such as brachiopods  
593 (Baliński 2002; Curry and Brunton 2007) were less affected and remained quite diverse  
594 despite extinction as they recovered quickly. In addition, no strong increase of the trilobite  
595 morphological disparity occurred in the Famennian. Hence, the Late Devonian events led to  
596 bottleneck periods for the trilobites but also for other organisms such as diplobathrid crinoids,  
597 which vanished in the Carboniferous after having come close to extinction in the Devonian  
598 (Cole & Hopkins 2021). This trend suggests that trilobites were a major clade during the first  
599 half of the Palaeozoic but not at the end-Palaeozoic although they survived until the Permian  
600 with few periods of diversification (Lerosey-Aubril and Feist 2012).

601

## 602 **Conclusion**

603

604 Trilobites proliferated in North Africa during the Devonian. As globally, there was an  
605 important Early Devonian diversification, which led to both an increase of taxonomic richness  
606 and morphological disparity. Several innovations occurred (development of spines for  
607 instance), facilitated by favourable environmental conditions and fluctuating ecological  
608 conditions. Because the Early Devonian diversification involved families already existing for

609 several million years, most of the Devonian trilobite families had a bottom-heavy dynamic  
610 characterized by a late diversification. Coupled increases in diversity and morphological  
611 disparity are not common in the fossil record and can be explained by higher morphological  
612 constraints in the late evolutionary history of the clade. However, this coupling could result  
613 from the multiple extinction events, which occurred in the Middle and Late Devonian and  
614 prevented the long-term increase in disparity. Indeed, the Middle and Late Devonian events  
615 affected North African trilobites and the diversity decreased since the Eifelian. At the same  
616 time, there was an important loss in morphologies, but the majority of losses occurred later, in  
617 the Givetian. A lateral extinction occurred with the preferential disappearance of genera  
618 located **at the edge** of the morphospace. This pattern indicates non-random extinctions in the  
619 context of environmental changes, including sea-level variations. After the Kellwasser events,  
620 another diversification occurred in the Famennian, of a less intensity. However, despite strong  
621 morphological variations throughout the Devonian, trilobites conserved a relative uniform  
622 size and no real ‘Lilliput effect’ occurred after extinctions. Because the trilobites survived for  
623 a long time at low level of diversity in the Middle and the Late Devonian, we can consider  
624 them as a ‘dead clade walking’.

625

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636

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638

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994

## 995 **Figures**

996

- 997 **Figure 1.** (A) Geographical location of Devonian outcrops of North Africa (from [Hollard,](#)  
998 [1968](#)) and (B) complete chimeric exoskeleton of trilobite in dorsal view exhibiting eight

999 landmarks for cephalon (in red), plus eight for cranidium (in blue), and seven for pygidium (in  
1000 black); and some linear measurements. Modified from Crônier (2013).

1001

1002 **Figure 2.** Diversity dynamics of Silurian and Devonian trilobites from North Africa. Number  
1003 of genera per stage represented in each structure are represented in blue for cephalon; red for  
1004 cranidium and black for pygidium. Modified from Crônier (2013). Ages from Cohen et al.  
1005 (2013, v. 3/2020).

1006

1007 **Figure 3.** Morphological disparity indices according each structure of Silurian and Devonian  
1008 trilobites from North Africa. Indices used are Sum of Ranges (SoR); Sum of Variance (SoV);  
1009 and the nearest Neighbour Distance (NND) and displayed for each stage.

1010

1011 **Figure 4.** Centroid size through time of Silurian and Devonian trilobites from North Africa  
1012 for each structure (i.e., cephalon; cranidium and pygidium). Boxes represent interquartile  
1013 ranges (IQR) and bars correspond to 1,5IQR. Values being outside the 1,5IQR are depicted  
1014 by dots. Sample size is noted under each box plot.

1015

1016 **Figure 5.** Diversity-disparity space (Jablonski, 2017) of the relation between taxonomic and  
1017 morphological diversification of Devonian trilobites from North Africa. Type 1: Dominance  
1018 of morphological diversification; Type 2: Morphology concordant with taxonomic  
1019 diversification; Type 3: Dominance of taxonomic diversification. Abbreviations: S.: Silurian,  
1020 L.: Lochkovian, P.: Pragian, E.: Emsian.

1021

1022 **Table 1.** Correlation results between diversity and each morphological disparity index. P  
1023 values adjusted and Kendall's tau for each structure are displayed.

1024

1025 **Supplementary data**

1026

1027 **Figure S1.** Description of landmarks.

1028

1029 **Figure S2.** Morphospace occupancy through time of the Silurian–Devonian trilobites from  
1030 North Africa (two first principal component axes only). (A) cephalon; (B) cranidia; and  
1031 (C) pygidia.

1032

1033 **Figure S3.** Diversity dynamics of Silurian and Devonian trilobites from North Africa  
1034 measured with the shareholder quorum sampling (SQS, [Alroy 2010b](#)). Number of  
1035 genera per stage represented in each structure are represented in blue for cephalon; red  
1036 for cranidium and black for pygidium. Modified from [Crônier \(2013\)](#). Ages from [Cohen](#)  
1037 [et al. \(2013, v. 3/2020\)](#).